

FINE-SCALE INTERTIDAL DISTRIBUTION AND RECRUITMENT PATTERNS
OF THE GUMBOOT CHITON *CRYPTOCHITON STELLERI*
(POLYPLACOPHORA: MOPALIIDAE)

Joshua P. Lord

Oregon Institute of Marine Biology, P.O. Box 5389, Charleston, Oregon 97420, U.S.A.;
lord@uoregon.edu

ABSTRACT

The gumboot chiton *Cryptochiton stelleri* Middendorff, 1847, is the largest intertidal invertebrate herbivore in the northeast Pacific, but little is known about the fine-scale distribution of this species within its range. In this study, extensive intertidal surveys were used to determine the distribution of *C. stelleri* within six rocky intertidal sites on the southern coast of Oregon, USA, and found that gumboot chitons show a patchy and clumped distribution. At all six sites, individuals were found at highest densities within small coves, and small specimens (< 15 cm long) were found almost exclusively in sea urchin pits. Age-frequency histograms were created for populations of *C. stelleri* at all six sites and showed sporadic cohort success, likely as a result of sporadic recruitment. Successful cohorts were indicated by peaks in the age-frequency histograms and were compared between sites in order to determine whether or not successful cohorts occurred at the same time at all sites. There was low similarity between sites, and a negative correlation was found between distance between sites and percent similarity in age-frequency peaks. Combined with other factors, this suggests that larval settlement and cohort success of *C. stelleri* is driven by local factors, not such large-scale factors as upwelling or El Niño.

Key words: population structure, abundance, density, cohort, mollusk.

INTRODUCTION

Intertidal herbivores can have significant ecological impacts on the algal composition and overall species assemblages on rocky shores around the world (Lubchenco, 1978; Moreno & Jaramillo, 1983; Dethier & Duggins, 1984; Jenkins & Hartnoll, 2001). Chitons, such as *Katharina tunicata*, have widespread direct and indirect effects on the population dynamics of the rocky shore by altering macroalgal density (Dethier & Duggins, 1984). *Katharina tunicata* and urchins, such as *Strongylocentrotus purpuratus* and *Strongylocentrotus droebachiensis*, can completely change the surrounding community by causing shifts in habitat type (Leighton et al., 1966; Moreno & Jaramillo, 1983; Himmelman, 1984; Dethier & Duggins, 1984; Chapman & Johnson, 1990). These effects are strongly influenced by population density, since areas of high herbivore density are most dramatically affected (urchin barrens, e.g.).

The ecological impact of high herbivore density highlights the importance of distribution and population structure in community ecology.

Density affects not only the food intake of the population, but also its reproductive capacity. Many species must sustain a minimum density in order to be reproductively successful, including barnacles (Kent et al., 2003; Munroe & Noda, 2009), mussels (Downing et al., 1993), urchins (Levitan et al., 1992), and some plants (Kunin, 1997). For example, the sea palm *Postelsia palmaeformis* is unlikely to persist at low population densities due to limited gamete dispersal (Dayton, 1973; Paine, 1988). Density can be especially important for free spawning species, because a critical concentration of sperm is needed for successful fertilization of eggs (Levitan et al., 1992; Young et al., 1992).

Despite the ecological importance of population density and structure for such large intertidal herbivores as *K. tunicata* and *S. purpuratus*, nothing is known about the fine-scale (within site) distribution of the gumboot chiton *Cryptochiton stelleri* Middendorff, 1847 (Petersen & Johansen, 1973; Palmer & Frank, 1974; Yates, 1989). This species is the largest intertidal invertebrate herbivore in the northeast Pacific and is a common inhabitant of rocky intertidal

shores from California to Alaska, Kamchatka, and Japan. It is a generalist herbivore, feeding on the blades of algal genera *Mazzaella*, *Cryptopleura*, *Nereocystis*, *Saccharina* and *Ulva*, but preferring *Mazzaella* and *Cryptopleura* (Heath, 1905; Yates, 1989). As such, *C. stelleri* could affect macroalgal abundance in its intertidal and subtidal (down to 60m) habitat and create space for limpets or other grazers in a similar manner to the leather chiton *K. tunicata* (Dethier & Duggins, 1984).

The distribution of *C. stelleri* could be influenced by seasonal changes in food availability, wave action, temperature or other factors (Yates, 1989). Snow (1951) suggested that this species may move to lower intertidal and subtidal areas in the winter and back up in the spring and summer. This type of vertical migration in the intertidal and subtidal zones has been tied to seasonal differences in food availability for the green crab *Carcinus maenas* (Hunter & Naylor, 1993) and several species of limpets (Branch, 1975). Tidal level migration can also occur over a lifetime in some species, such as intertidal snails *Chlorostoma funebris* (Paine, 1969) and *Monodonta labio* (Takada, 1996). The prevalence of either seasonal or

lifetime vertical migration patterns in other mollusks indicates the possibility that these changes in distribution occur with *C. stelleri*.

The present study maps the intertidal distribution of all post-larval life stages of *Cryptochiton stelleri*, including juveniles, which are reportedly extremely rare (Tucker & Giese, 1962; MacGinitie & MacGinitie, 1968; Palmer & Frank, 1974; Yates, 1989). Only 12 individuals less than 15 centimeters in length and only three juveniles were discovered in a five-year feeding study of *C. stelleri* by Yates (1989). The present study also assessed the population structure of several southern Oregon intertidal populations of *C. stelleri*. These distribution and population structure data were used to test the existence of seasonal or ontogenetic vertical migration patterns for this chiton species. The aim of this study was to understand what factors influence the fine scale (within site) intertidal distribution, abundance and recruitment patterns of *Cryptochiton stelleri*.

MATERIALS AND METHODS

Distribution

In order to determine the local distribution, size frequency, and population sizes of *Cryptochiton stelleri* along the southern Oregon coast, surveys were conducted at six sites (Fig. 1). The southernmost of the sites surveyed was Cape Blanco, Oregon (42°50.900'N, 124°33.410'W), a basaltic rocky shore with intertidal areas facing to the northeast, west, and south. All other sites were located just south of Charleston, Oregon (43°18.191'N, 124°23.198'W). Middle Cove of Cape Arago is mostly composed of sandstone boulders and is a relatively protected intertidal area that faces west and has very little foot traffic. South Cove of Cape Arago is a similar intertidal to Middle Cove, though it faces south and has more foot traffic. Sunset Bay is another protected site with high foot traffic and is a small, west-facing bay with a long flat sandstone intertidal bench interspersed with deep tidal channels. Qochyax Island has very little foot traffic and an extensive rocky intertidal area that includes both exposed and protected areas. Lighthouse Island is fairly exposed on the south-facing side and moderately protected on the north-facing intertidal and also has low foot traffic.

The intertidal zones at these sites were sampled from July 2009 to August 2010, on every

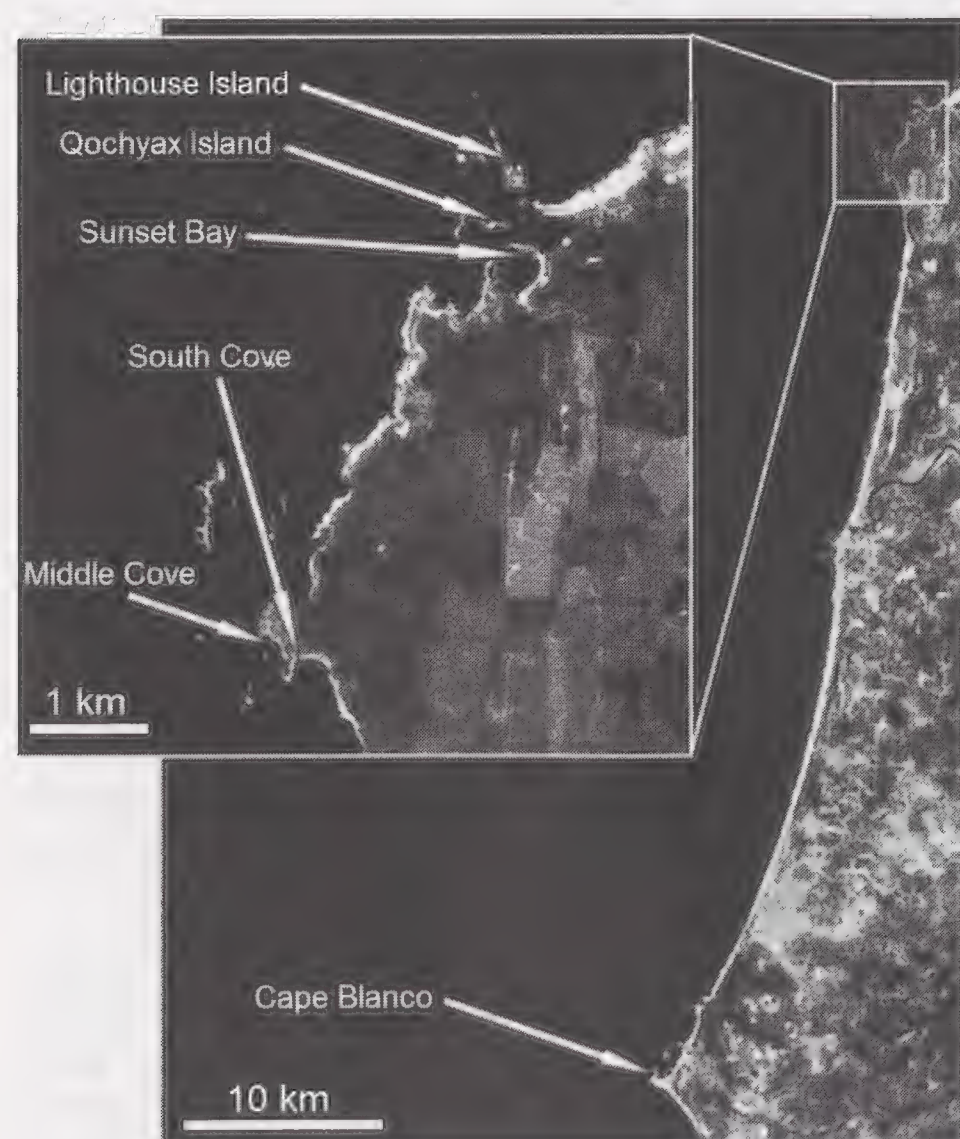


FIG. 1. Locations of all six sites on the southern Oregon coast (north to south): Lighthouse Island, Qochyax Island, Sunset Bay, Middle Cove, South Cove, Cape Blanco.

tide below -0.3 m MLLW, weather-permitting. *Cryptochiton stelleri* were found via extensive (2–3 days per site) systematic searches that were conducted by walking perpendicular to the shoreline from the low water level to the top of the intertidal zone and then back down. With this method, the entire intertidal zone was searched at all sites, since the surveyor passed within 2 meters of every intertidal location. This broad search method was necessary because of the patchy distribution of this species and was appropriate because the goal of this study was to determine distribution over entire sites and not to estimate population size. Once *C. stelleri* were discovered, their exact locations were recorded by triangulation with known landmarks using a compass accurate to 0.1 degrees. This produced coordinates with a maximum error of 1.5 m for the location of each individual. Body volume was then measured to the nearest 5 mL using water displacement in a 4-liter graduated plastic container.

Individual *Cryptochiton stelleri* specimens were tagged at South Cove, Middle Cove, Cape Blanco, and Lighthouse Island in order to detect growth and seasonal movement patterns of individuals. Animals were tagged by inserting zip ties through the edge of the girdle and attaching numbered monel fish tags (National Band and Tag Co.). Zip ties were short (10 cm) and excess tie length cut off after attachment. This method of tagging is similar to that used by Palmer & Frank (1974), who used monofilament line through the girdle and marked with beads. It is also similar to Yates (1989), who used spaghetti tags, also through the girdle. After marking, *C. stelleri* usually rolled up into a ball but resumed normal movement minutes after being placed back in their original location. Individuals were observed until they reattached to the substratum.

Distribution data obtained via triangulation methods were entered using Google Earth® with overlaid infrared aerial photos of the intertidal zone taken by the Oregon Department of Fish and Wildlife (1:7200 scale). These data were then transferred into ArcMap® software and converted into GIS layers. To determine the amount of clumping at different sites, data were analyzed in ArcMap® using the spatial analysis tool “nearest neighbor”. This tool calculated the expected mean distances between individuals if their distribution was random and compared this to the observed mean distances between individuals. Getis-Ord General G, another spatial analysis tool, was used to determine

if individuals were clustered by size at each intertidal site. This GIS software was also used to analyze variation in distributions at all sites between each sampling date in order to compare tidal and seasonal differences in the distribution of individuals.

To determine whether or not several intertidal predators could consume *C. stelleri*, sea stars *Evasterias troschelii*, *Pisaster ochraceus*, and *Pycnopodia helianthoides* and crabs *Pugettia producta* and *Cancer productus* were kept together in a 1m x 2m flowing seawater tank for two months with just *C. stelleri* individuals ranging from 10 to 30 cm in length as potential prey items.

Age-Frequency

Volume was converted to age based on data derived from growth lines in the shell plates of *C. stelleri* (Lord, in review). A growth function relating age to volume was fit to these data and was used to estimate age for all surveyed gumboots. Age-frequency histograms were then created for each site and each season and peaks (possible cohorts) in these histograms were compared between sites and sampling dates. Each peak (cohort) in these data were identified using Peakfit® software and major peaks were defined as those at least two times the average number of individuals of each age for each site. Major peaks were then compared between sites in order to determine how uniform recruitment and survival were in *C. stelleri*.

RESULTS

Distribution

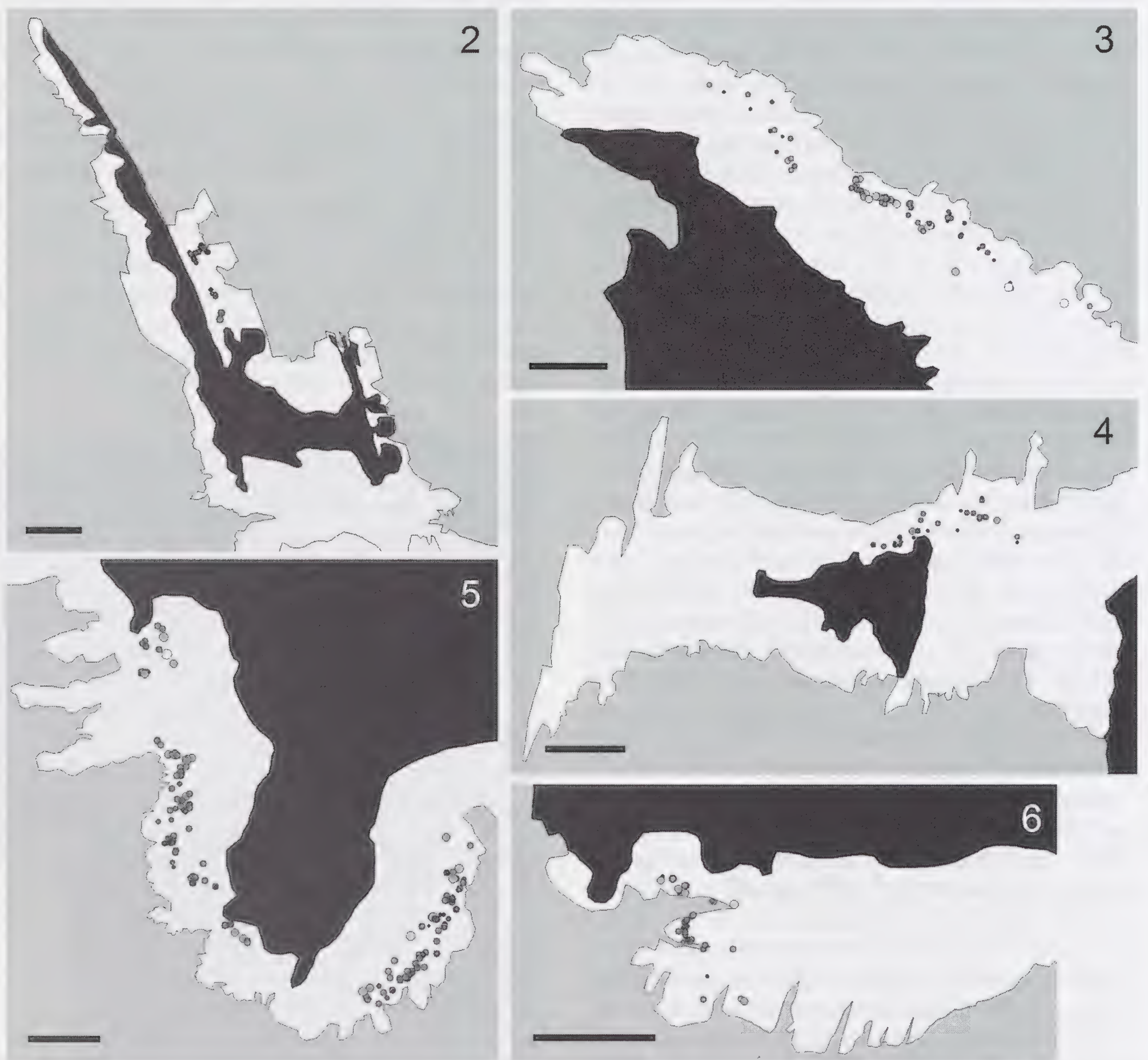
Field surveys showed a patchy distribution of *C. stelleri* at all six surveyed sites (Figs. 2–6). Average nearest neighbor distance showed significant ($p < 0.05$) clumping at Cape Blanco, South Cove, Middle Cove, Sunset Bay, and Lighthouse Island. Slightly less clumping was found at Qochyax Island (Fig. 5), but this was likely a result of the small area in which *C. stelleri* was found. Nearest neighbor statistics only included areas where *C. stelleri* was present, so did not take into account large areas where no individuals were found. Qochyax Island had a limited area in which *C. stelleri* was present, but within this area there was not a significant amount of clumping ($p = 0.1$). There were no

individuals of this species present in areas of very high wave action at any sites, as none were found in the outer areas of Lighthouse Island (Fig. 2), Cape Blanco (Fig. 3), Cape Arago (Fig. 4), Qochyax Island (Fig. 5) or Sunset Bay (Fig. 6). Gumboot chitons were found almost exclusively in small coves within sites (Figs. 4, 6) or in northeast-facing habitats (Figs. 2, 3, 5).

Populations were also clumped based on size at several of the sites (Figs. 2–6). Getis-Ord G High/Low clustering analysis showed significant ($p < 0.05$) clustering of large individuals

(by volume) at Qochyax Island, Lighthouse Island, South Cove and Cape Blanco. Clustering based on size was not significant at Middle Cove and Sunset Bay. Few individuals of *C. stelleri* were found in areas of high sand scour, evidenced by the lack of individuals near beaches in the interior of Lighthouse Island, South Cove, Sunset Bay and Cape Blanco.

Eighty-five of 92 specimens shorter than 15 cm in length were found in (mostly) abandoned pits of urchins (*Strongylocentrotus purpuratus*) at all six sites. The seven not found in pits were juveniles less than 2 cm in length. Three of



FIGS. 2–6. Size and distribution of *Cryptochiton stelleri* at all sites surveyed in May 2010. Size and lightness of circles are relative to the size of the specimens; small dark circles represent small gumboot chitons and large white circles represent the largest gumboot chitons. Light gray fill represents the ocean, white is intertidal, and dark gray is terrestrial. Scale bar = 50 m. FIG. 2: Lighthouse Island; FIG. 3: Cape Blanco; FIG. 4: Middle Cove (on left) and South Cove (on right) of Cape Arago; FIG. 5: Qochyax Island; FIG. 6: Sunset Bay.

these were in small holes made by boring clams and near the leafy red alga *Cryptopleura*. The remaining four juveniles were on flat surfaces within a bed of *Cryptopleura*, which is their preferred food source (Lord, in press). All juveniles were found below -0.3 m MLLW. Of the over 300 *Cryptochiton stelleri* specimens that were tagged, only 41 were found six months later due to the propensity of the tags to fall out of the girdle. Many specimens were found with marks where a tag had been previously, though they were soon indiscernible because of the rapid healing process of *C. stelleri*. There was not a significant difference between sites in the distance moved between November 2009

tagging and May 2010 recovery, although the range was higher at South and Middle Cove than Sunset Bay. South Cove ($n = 19$) and Middle Cove ($n = 12$) chitons had ranges of approximately 3 to 22 meters traveled, while Sunset Bay ($n = 9$) chitons were between 3 and 12 meters from their initial location.

Distributions did not change noticeably at Middle or South Cove of Cape Arago (Figs. 7, 8) or at Sunset Bay (Figs. 9, 10) between November 2009 and May 2010. These three sites are shown because they were the only three surveyed during November due to high wave activity. The “directional distribution” tool in ArcMap® created standard deviation ellipses for each population during each season and these maps indicated that there was no consistent pattern of population movement with season at these site.

In the predation experiment, no *C. stelleri* were eaten by any of the predators over a two-month period. All *C. stelleri* remained attached to the bottom and sides of the tank, never falling off or lying upside-down like they do occasionally in the intertidal zone at low tide. This is relevant, because in the intertidal *C. stelleri* often uses aerial respiration at low tide, during which they expose their gills and often fall off rocks, thus exposing their muscular foot to potential predators.

Age-Frequency

All surveyed *Cryptochiton stelleri* specimens were estimated to be between one and 40 years old. These estimates were based on growth curve data (Lord, in review) for *C. stelleri* that show a good regression between age and size. Age-frequency histograms at all sites showed the highest number of individuals at intermediate ages. While close to 100 young (< 15 cm) *C. stelleri* individuals were discovered in all seasons, the cryptic nature of these age classes and their urchin pit habitat makes it very likely that specimens less than 10 years of age are underestimated in these age-frequency histograms. This did not adversely affect peak fitting because relative peaks still appeared at young ages. Major peaks ($> 2 \times$ average number) were compared between sites and there was no major peak that was present at a specific age at all sites, although a few peaks were shared by multiple sites (Figs. 11–16). Peaks at 22 and 24 years old were present to some extent at all sites except Cape Blanco. Sunset Bay, Qochyax Island and Lighthouse Island shared a major peak at 16 and 20 years

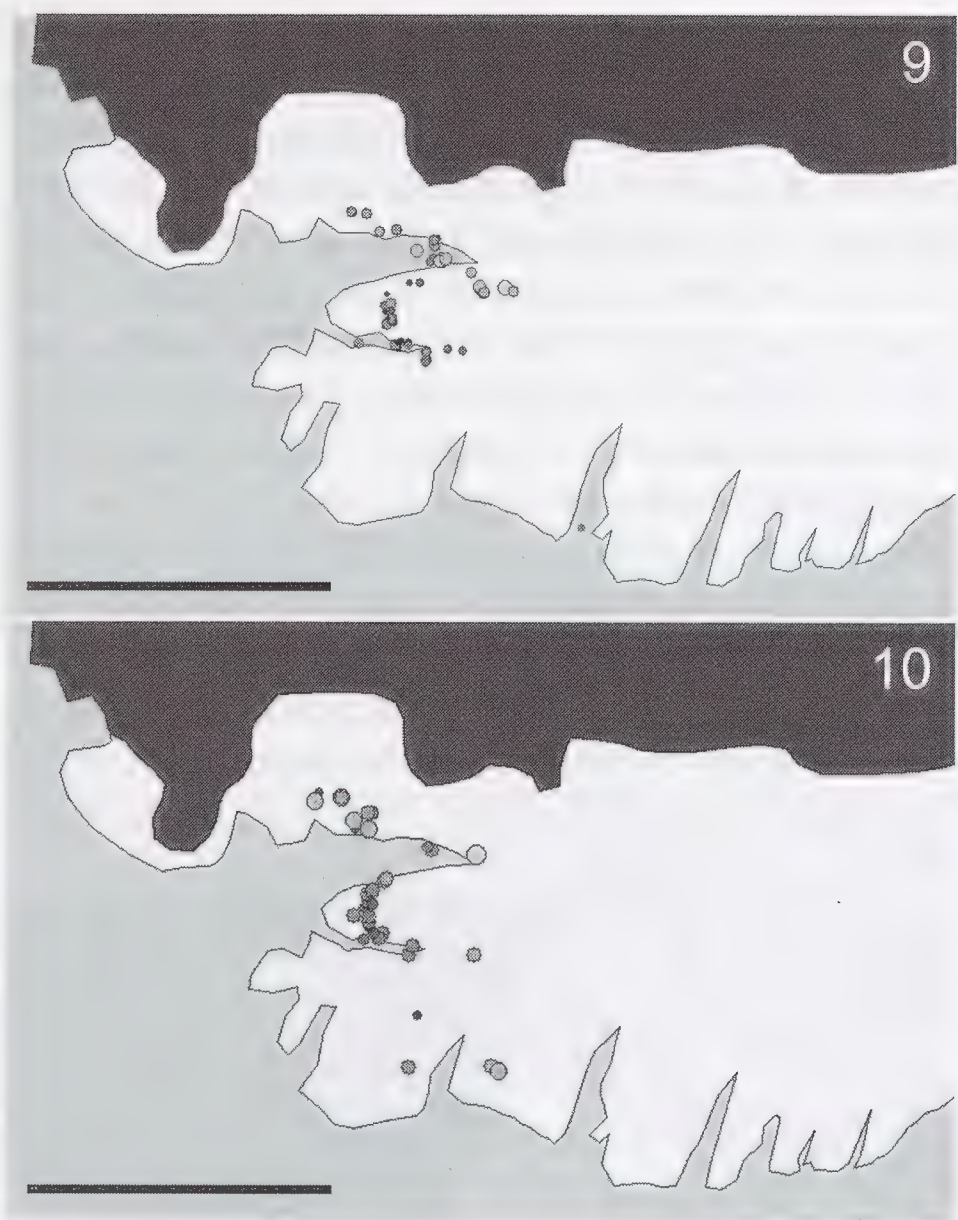


FIGS. 7, 8. Distribution of *Cryptochiton stelleri* at Middle and South Cove of Cape Arago. Distribution did not change noticeably with season. Scale bar = 50 m. Light gray fill represents the ocean, white is intertidal, and dark gray is terrestrial. FIG. 7: November 2009; FIG. 8: May 2010.

(Figs. 11, 14, 16). Cape Blanco, Middle Cove, and Sunset Bay shared peaks at 30 years (Figs. 12, 13, 16) but few other peaks were shared between more than two sites. Distance was measured as a straight line between sites, and similarity was calculated as the number of shared peaks over the number of total peaks for each pair of sites.

There was a significant correlation between the number of shared peaks and the $\log_{10}$ of distance between sites (Pearson's correlation coefficient, $r^2 = 0.46$, $t = -3.34$, $df = 13$, $p < 0.01$) (Fig. 17). The distances were $\log_{10}$ transformed because all of the sites were relatively close together with the exception of Cape Blanco, which would make a test of correlation impossible. The two sites with the highest percentage (66%) of peaks in common were Sunset Bay and Qochyax Island, which were the closest sites to each other, at 0.37 km (Table 1). The second most similar sites (60%) were South Cove and Middle Cove of Cape Arago, which were 0.38 km apart. The northern-most site, Lighthouse Island, did not share any peaks with the southern-most site, Cape Blanco. Cape Blanco only shared an average of 21% of its age-frequency peaks with other sites, all of which were at least 50 km north of Cape Blanco. The closest site to the north of Cape Blanco was South Cove, which was the most similar site to Cape Blanco in terms of age-frequency peaks, at 40% (Fig. 17, Table 1).

No correlation ($p > 0.4$) was found between upwelling start date or strength and age-frequency histogram peaks or gaps. There was

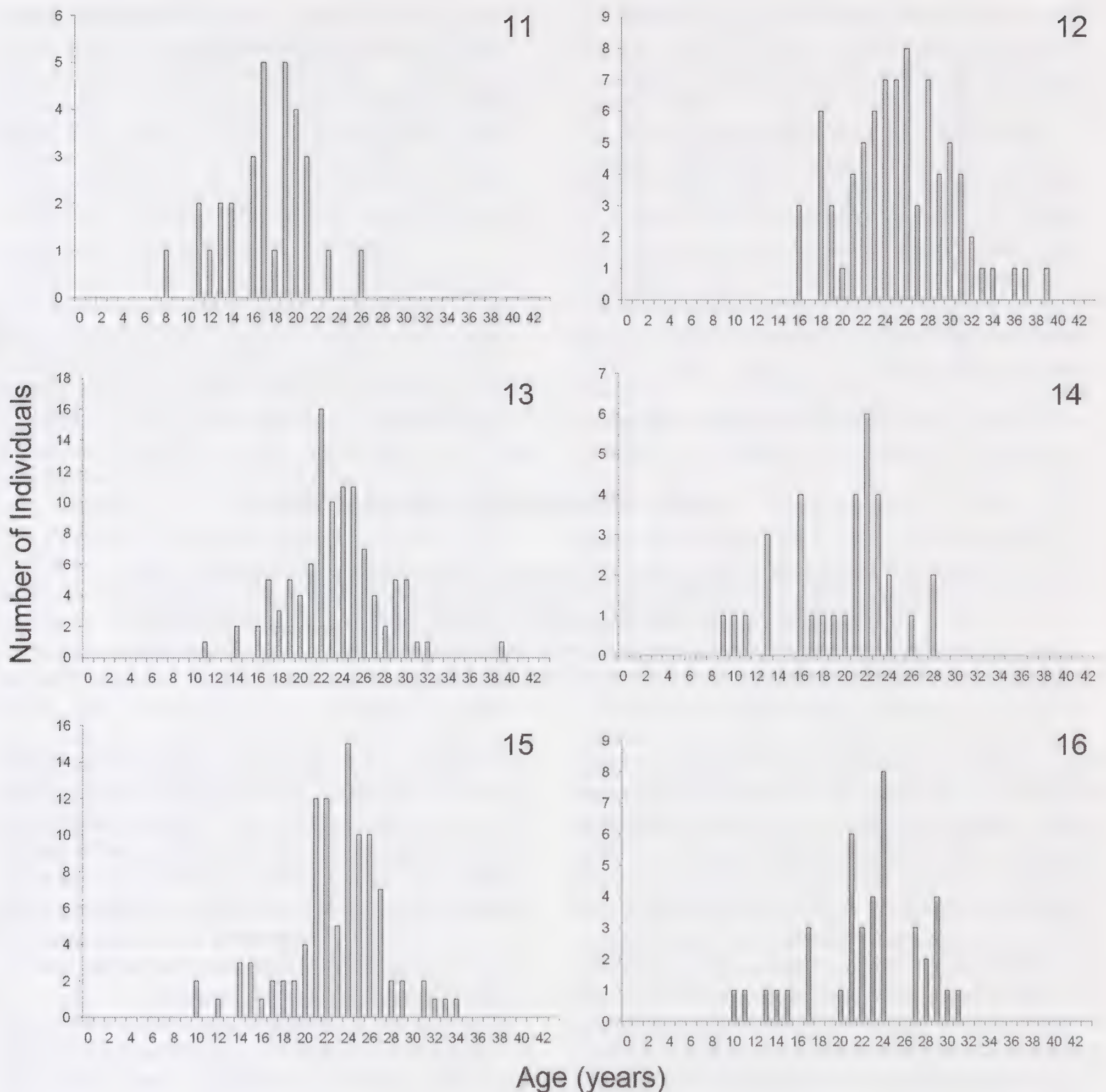


FIGS. 9, 10. Distribution of *Cryptochiton stelleri* at Sunset Bay. Like at Cape Arago, distribution did not change noticeably between seasons. Scale bar = 50 m. Light gray fill represents the ocean, white is intertidal, and dark gray is terrestrial. FIG. 9: November 2009; FIG. 10: May 2010.

also no correlation ($p > 0.4$) between El Nino years and the peaks or gaps in age-frequency histograms at any of the sites.

TABLE 1. Distances and similarities in age-frequency peaks between six different sites on the southern Oregon coast. There is a significant negative correlation between the distance and similarity between sites. Sites are arranged north to south in both columns and rows, with Lighthouse Island the northern-most site and Cape Blanco the southernmost.

Sites	Lighthouse Island	Qochyax Island	Sunset Bay	Middle Cove	South Cove	Cape Blanco	
Lighthouse Island	X	0.58 0.44	0.89 0.22	4.67 0.44	4.83 0.22	57.9 0.00	Distance (km) Similarity (%)
Qochyax Island		X	0.37 0.66	4.19 0.22	4.25 0.22	57.3 0.22	Distance (km) Similarity (%)
Sunset Bay			X	4.00 0.40	4.07 0.40	57.06 0.20	Distance (km) Similarity (%)
Middle Cove				X	0.38 0.60	53.2 0.20	Distance (km) Similarity (%)
South Cove					X	53.1 0.40	Distance (km) Similarity (%)



FIGS. 11–16. Age-frequency histograms for all six sites surveyed in May 2010. No peaks are shared between all sites, although most sites have a peak at around 20–22 years. The lack of young individuals is partially a result of their cryptic nature. FIG. 11: Lighthouse Island; FIG. 12: Cape Blanco; FIG. 13: Middle Cove; FIG. 14: Qochyax Island; FIG. 15: South Cove; FIG. 16: Sunset Bay.

DISCUSSION

The patchy distribution of *Cryptochiton stelleri* at each of six sites (Figs. 2–6) raises several questions about the life history and ecological impact of this species. It is not surprising that *C. stelleri* specimens were not found in areas of high wave action or high sand scour because these types of habitat generally do not have the types of thin bladed seaweeds upon which *C. stelleri* feeds. In addition, *C. stelleri* does not clamp to the substratum with the same force

and tenacity that *Katharina tunicata* or other wave-tolerant chitons do, and is often found unattached to the substratum at low tide (pers. obs.). Therefore, it is likely that both physical and dietary limitations result in the absence of *C. stelleri* in areas of high wave action or sand scour.

However, the clumped distribution of *C. stelleri* found by this study was present at sites where this species is abundant (Figs. 2–6), so the clumped distribution is not likely due to sand scour or extreme wave action. Sand

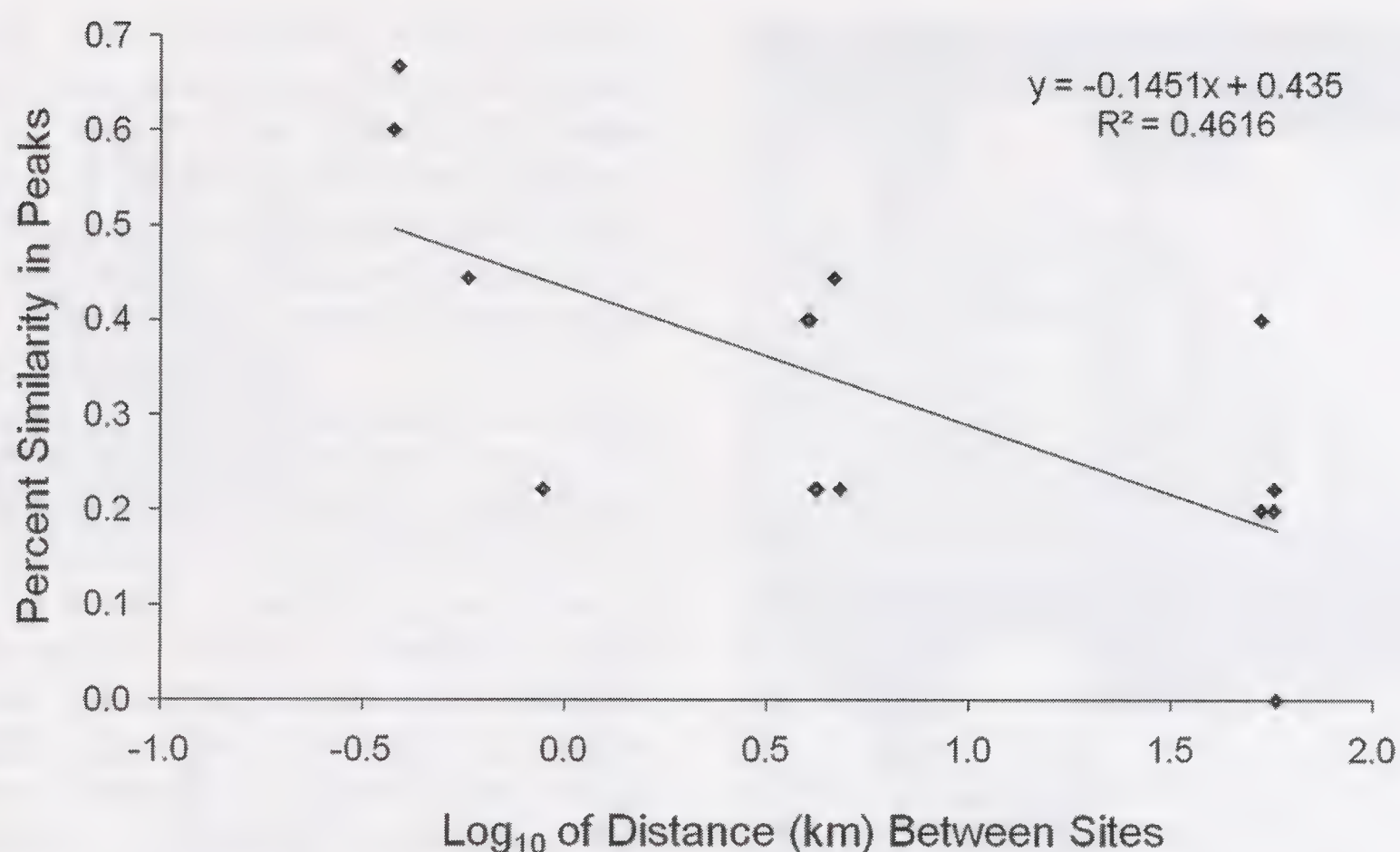


FIG. 17. Distances ($\log_{10}$ km) and similarity in age-frequency peaks between six different sites (15 pairs of sites). Distances were $\log_{10}$ transformed in order to compare between sites since five sites were relatively clumped (within 10 km) and the sixth site was approximately 55 km south of the others. Correlation coefficient and equation of the best fit line are shown.

scour generally occurred at the edges of the surveyed sites and wave action is similar within protected sites, so these factors are not likely to influence distribution within these sites. A clumped distribution is not unusual for chitons (Grayson & Chapman, 2004; Connelly & Turner, 2009). During spring, summer and fall, leafy red algae such as *Cryptopleura* and *Mazzaella splendens* and greens such as *Ulva lactuca* are abundant throughout all sites surveyed. Therefore, the clumped distribution of *C. stelleri* is not due to food distribution. Distribution patterns are also unlikely to be driven directly by predation, since *C. stelleri* was not eaten by any predator. Sea stars *Evasterias troschelii*, *Pisaster ochraceus*, and *Pycnopodia helianthoides* and crabs *Pugettia producta* and *Cancer productus* did not feed on *C. stelleri* in this study, though field observations have been made of sea stars consuming *C. stelleri*. It is likely that sea stars and crabs can consume *C. stelleri* if it becomes detached from the rocks, exposing the muscular foot.

It seems more likely that *C. stelleri* is limited to protected areas even within sites in order to avoid being dislodged from the rocks. Dislodgement could result in mortality from wave action or increased predation risk. Gumboot chitons were most common in small coves within sites, especially at Lighthouse Island (Fig. 2), Middle Cove (Fig. 6), and Sunset Bay (Fig. 4). Because

C. stelleri under 15 cm in length were found almost exclusively in abandoned sea urchin pits, it is also possible that the distribution of small *C. stelleri* is driven by the presence of these pits. With smaller individuals limited to these cryptic habitats and large individuals able to move at least 20 meters, this could explain the clumping of large individuals in areas where small specimens are not present.

The cue for settlement and metamorphosis for *C. stelleri* is encrusting coralline algae (Lord, in press), which is ubiquitous throughout all sites so is not a limiting factor in the settlement or recruitment of *C. stelleri*. However, urchin pits are largely covered in encrusting coralline algae because of macroalgal grazing by *S. purpuratus* and could serve as a good spot for *C. stelleri* to settle and survive. The small coves with high densities of *C. stelleri* could be acting as larval traps where slower, swirling water allows larvae to settle out of the water column. Settlement and recruitment in small coves may also lower mortality rates of new recruits and juveniles which are undoubtedly susceptible to wave bashing. If urchin pits act as a nursery for young individuals, this would explain the pattern of large *C. stelleri* being clumped, since areas without urchin pits are only going to be occupied by large individuals that have moved there later in life. Clumps of large individuals could have a great impact on

macroalgal abundance at least on a fine scale, given that smaller herbivores, such as *Katharina tunicata* (Dethier & Duggins, 1984) and *Strongylocentrotus purpuratus* (Leighton, 1966; Estes & Duggins, 1995) can greatly affect algal assemblages. Seaweed consumption could be especially high in these adult high density areas because *C. stelleri* food intake scales linearly with body volume (Lord, in review).

While *C. stelleri* will move out of the urchin pits over the course of their lives, they do not display seasonal variation in distribution (Figs. 7–10) and do not move up or down in the intertidal with age. Snow (1951) mentioned that *C. stelleri* move down in the intertidal during the winter and then up during the spring. This has been described in a variety of other species, including crabs (Hunter & Naylor, 1993) and several species of limpets (Branch, 1975). However, year-round surveys in the present study did not reflect this pattern at any of these southern Oregon sites. There were also no vertical patterns in size or age of *C. stelleri* like those shown in *Chlorostoma funebris* (Paine, 1969) and *Monodonta labio* (Takada, 1996). The lack of vertical migration with season by *C. stelleri* may be due to its ability to go months without eating (Yates, 1989) or to the fact that it already inhabits fairly protected habitats. By living in protected areas, there may be no need for *C. stelleri* to move up or down in the intertidal zone to avoid the intense wave action from winter storms in Oregon.

More about larval settlement patterns can be ascertained from age-frequency data (Figs. 11–16) for each site and similarity in cohort peaks within age-frequency distributions between sites (Table 1). The success of these large cohorts (peaks) could be due to high recruitment or to low mortality at some life stage. It is unlikely that predation on adults would vary greatly between cohorts, so the most likely causes of the variation between cohort sizes are differences in settlement or juvenile survival. While predation experiments have not been done with juvenile *C. stelleri*, it is likely that crabs and sea stars or even fish could easily detach and consume these small individuals with tiny plates. Therefore, a good recruitment year for any of these predators could cause high juvenile mortality for *C. stelleri*. However, population levels of *C. stelleri* are not very high compared to other species of mollusks and young individuals are found in small protective pits, so it is unlikely that any life stage of *C. stelleri* is the primary food source for any predator.

Therefore, the most likely cause of variations in cohort size is larval supply and settlement success. This species of chiton spawns annually (Tucker & Giese, 1962; Lord, in press) and has lecithotrophic larvae. Differences in number of planktonic predators could have an impact, since larvae can remain competent for up to two months even though they can settle and metamorphose in as few as five days after spawning (Lord, in press). Oceanographic conditions, such as the directions of currents, could affect settlement as well, as could wave action or other small-scale near-shore oceanography conditions. For example, populations may have successful self-recruitment when local barriers form and limit the movement of planktonic larvae out of a cove or bay. At several sites along the southern Oregon coast, upwelling can cause these barriers to form at the mouths of such coves as Sunset Bay, potentially trapping larvae inside and enhancing local recruitment (Shanks & McCulloch, 2003).

Shared peaks in cohort size between sites could be a result of either large-scale dispersal of larvae to multiple sites in the same period or local oceanographic conditions that enable successful settlement at multiple sites. No peaks were shared between all sites, and very few peaks were shared by more than three of the six sites, suggesting that successful cohorts were not driven by large-scale oceanography, because if that were the case then all sites would likely share peaks in the age-frequency histograms. There was also no correlation between upwelling strength or start date and the age-frequency histogram peaks or gaps. This suggests that local conditions are more likely to affect the success of a recruitment class or cohort. The significant negative correlation between the number of shared cohort peaks and distance between sites further supports this conclusion (Fig. 17). The high similarity in peaks between the closest sites (Middle Cove + South Cove, Sunset Bay + Qochyax Island) indicates that these sites either share larvae or have similar near-shore local oceanographic patterns (Table 1). There appears to be low population connectivity between sites, given the potentially short larval period of this species and the lack of shared peaks in age-frequency histograms, although genetic work is necessary to confirm this.

Limited larval supply, settlement, or high post-settlement mortality could also partially explain the relative scarcity of small *C. stelleri* reported by multiple studies (Tucker & Giese, 1962; MacGinitie & MacGinitie, 1968; Palmer

& Frank, 1974; Yates, 1989). However, these studies report a lack of individuals < 15 cm in length, or < 13 years old (Lord, in review), a span of ages too wide to be accounted for by sporadic recruitment. The present study found over 90 individuals in this "rare" size range, with several at every site, and almost all of them were in sea urchin pits or other holes in the rocks. In areas without sea urchin pits, young *C. stelleri* presumably occupy crevices or live under rocks in the low intertidal zone. It is very likely that the use of these cryptic habitats by young individuals is the reason why they are not found often. Juvenile *C. stelleri* are yellow unlike the dark red adults, which may also cause confusion.

Surveys in this study showed that the different life stages of *C. stelleri* prefer different microhabitats, with young (< 13 years) individuals occurring in cryptic habitats. They may choose these habitats to avoid predation or to avoid wave action, but their preference for these habitats coupled with the relatively low mobility of adults may enhance the clumped distribution of this species. Spatial and temporal differences in abundance and distribution are most likely a result of differential settlement and juvenile survival that are controlled by near-shore oceanography or other local factors. The resulting patchy distribution of *C. stelleri* may result in locally high algal consumption in areas of high density of this species within sites.

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